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SOCIAL CLASS MORTALITY

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THE history of interest in the effects of social and economic environment on mortality is a fascinating chapter of vital statistics. Writers in the epoch when slavery was the basis of industry had little to say on occupational mortality or morbidity. Galen, in his famous treatise on hygiene, said explicitly that it was not worthwhile laying down hygienic rules for people who could not follow them and confined himself to the needs of the wealthy classes. Ramazzini was the first writer explicitly to discuss the effects of occupation on health in a large number of classes. His treatise, admirably translated by Dr. Wright of Bryn Mawr, is a classic, but was written in a pre-statistical age. Indeed not much was done on a wide statistical front until the middle of the 19th century when the British medical statistician Farr began publishing rates of mortality in occupational or industrial groups. This became a regular feature of the English statistics and was done every ten years. Farr himself was primarily interested in the environmental or occupational factors of mortality but naturally compared groups of roughly the same social class. Thus he compares the clergy of the English Church with Roman Catholic priests, remarking that the latter had a high mortality at ages over 55—"perhaps," he writes, "the effects of celibacy

are then felt." He also contrasts shoemakers with tailors, the former having a much higher rate of mortality.

Farr's successors in office continued to give special attention to the occupational element and improved the classification. The difficulty was that industrial and occupational classifications are not identical. A man who keeps a tailor's shop or a man who sells boots may make neither clothes nor boots, yet he will industrially speaking be either a tailor or a shoemaker although occupationally speaking both may be doing the same job of work, viz. keeping accounts or persuading customers to buy goods. In days of small business, when men sold what they made, that was not perhaps very important; now it is fundamentally important. Whether a girl types the letters of a garage proprietor or of a manufacturing chemist is occupationally indifferent, but her industrial classification will be different. Great and successful efforts have been made to render the classification really occupational. Like all reforms it had a drawback, viz. to make backward comparisons difficult. At the same time, people became more interested in the correlates of occupation. That tailors had higher rates of mortality than clergy might be, indeed certainly was, a resultant of other factors than the higher morality and better working conditions of the clergy; after all—not that there were not glaring exceptions—the per capita incomes of clergy were higher than those of tailors. In 1911 the first serious attempt was made to classify all occupations by social-economic status. The attempt was renewed in each successive census and in 1931 the mortality rates of the wives of occupied males were also tabulated. Anybody can seen difficulties. Social status and income are correlated but the correlation is far short of unity. The social status of a professor of mathematics is no doubt higher than that of a saloon keeper, but, as Bernard Shaw once remarked, any prosperous publican would turn up his nose at the incomes of all mathematicians and pure brain workers. Then some important occupations can only be pursued in particular areas; miners are bound by geological facts; agricultural labor is not an important occupation in urban slums. However, in spite of difficulties and oddities of particular allocations, nobody doubts that on the whole the classification is good, that—to take only the main classes formed by the English General Register Office—we do have a descending scale of social-economic eligibility.

On the whole, the modern trend of opinion is to the conclusion that the social-economic rather than the direct occupational factors

are of primary importance. One reason is, of course, that the plague spots of industrial hazard, for instance the silicosis and the toxic dangers, such as plumbism, have been largely eliminated. The object of this paper is not to challenge what I believe to be a just opinion but to call attention to some no doubt minor but still important factors. As the reader may not be familiar with the classification, the general headings are given here. Social Class I purports to represent the professional and generally well-to-do section of the population, Class III the skilled worker, and Class V laborers and other unskilled workers, while Classes II and IV are intermediates comprising occupations of mixed types, or types not readily assignable to the classes on either side.

It is hardly necessary to remark that some purely occupational class differentiation exists; obviously members of Class I are not at risk of industrial poisoning while directors of railroad companies (Class I) are not exposed to the risk of being crushed which effects shunters (Class III). It is however true that risks of this kind do not form a

TABLE 1

Population per 1000 in each age group: England and Wales 1931

AGES	SOCIAL CLASS						TOTALS
	I	II	III	IV	V	Unoccupied	
16—	7	29	500	200	186	79	1000
20—	13	61	549	197	151	28	1000
25—	20	105	515	186	164	11	1000
35—	27	158	486	164	156	9	1000
45—	31	182	450	163	164	11	1000
55—	33	186	415	170	180	17	1000
65—	36	186	401	170	169	39.	1000
70—	37	182	399	162	149	71	1000

large proportion of the causes of death, e. g. accidents were responsible for 6 per cent of the deaths among all males aged 20-65 during 1930-1932, while for underground workers in coal mines the percentage was 11, for motor transport drivers the percentage was 9, and only 4 per cent of the deaths among engine drivers, railroad, were due to accidents. A point less often made is the difference of age constitution.

This is shown in Table 1, "unoccupied" being of course a heterogeneous group.

The table shows that there is a movement from class to class, a marked progression during the first half of working life from the lower to the higher social classes, and from middle age there is some regression to the lowest classes. Social Classes I and II showed an increase in the relative populations throughout the period of working life. The rate of increase was larger for Class II than for Class I, the proportion in these groups at ages 45-54 being respectively 6.3 and 4.4 times the proportion at ages 16-20. Up to age 25 the population of these groups is increased from the unoccupied class by the entrance into professions of students who have finished their training. These ex-students probably form an important proportion of the recruits to these classes at the early ages, but the largest relative increase in the size of these groups occurred at ages 35-44. The proportion in Class III, after a rise of 10 per cent at ages 20-24, decreased continuously throughout life. The proportion of the population in Social Classes IV and V decreased during early life and then increased. This change in trend is probably due to men taking lighter jobs because infirmity or age prevented these from continuing in strenuous occupations. The unoccupied group shows a steep fall in youth and an equally steep rise in later life. Beside those who are mentally or physically incapable of following an occupation, who together with those of independent means form about ten per thousand of the theoretically employable population aged 25-55, the unoccupied at the early ages have a large proportion of students who enter employment at a later age than the general population, and from age 55 this class includes the retired and those whose physical condition has compelled them to cease work.

The mortality by social class and age is shown in Table 2. The standardized mortality ratio (S. M. R.) is the percentage ratio of the deaths actually registered to the standard deaths calculated by applying the general mortality rates for all males in age groups 20-, 25-, 35-, 45-, 55-65, to the populations in the social classes.

The mortality of the unoccupied differs considerably from the other groups. The higher rates in earlier life were due to the inclusion in this group of those who were mentally and physically abnormal; the low rates at the older ages understate the true mortality since the deaths of males who were returned on the census schedule as retired are credited to their last occupation. The consequence of this is that the old age

TABLE 2

Death rates per 100,000: England and Wales 1930-1932

AGES	ALL MALES	SOCIAL CLASS I	II	III	IV	V	Unoccupied
16—	268	380	241	235	253	264	525
20—	328	334	283	308	330	336	776
25—	346	288	283	333	360	374	1018
35—	559	439	468	533	609	667	1137
45—	1114	984	1021	1070	1158	1302	1380
55—	2355	2237	2347	2318	2340	2535	1829
65—	4654	4549	4816	4689	4638	5105	1719
70—	7441	6883	7948	7705	7823	8581	1708
S. M. R. (20-65)	100	90	94	97	102	111	135

mortality of the five social classes tends to be slightly overstated. The progression shown by the standardized mortality ratio for ages 20-65 is not shown by the mortality of the age groups until ages 35-44. Social Class I has the highest mortality at ages 16-19; the second highest at ages 20-24, being only slightly better than the worst; the second lowest at ages 25-34. At ages 16-24 accidents were responsible for two fifths of the mortality of Social Class I but only one fifth of the deaths in the remaining social classes were due to this cause. The excess of accidents in Social Class I was contributed by commissioned officers of the forces, mainly the air force. If commissioned officers are omitted from ages 20-24, the mortality is reduced from 334 to 275, and this rate is slightly less than that for Social Class II, 283, the lowest rate. The exclusion of commissioned officers from ages 16-19 does not materially affect the rate for Class I; it is reduced only from 380 to 370. The mortality from all causes less accidents for this age group is 257 and is higher than the all causes rate of Social Classes II to IV. This high rate is rather curious since it seems probable that the population at risk has enjoyed the social and environmental conditions associated with Class I all their lives as they entered it in the youngest age group.

The effects of the changing constitution of the social classes on mortality are rather speculative but it is certain that there is some selection as regards general health, some occupations demanding a

high standard of physique while others have no such restrictions. As a consequence the populations of the latter groups are, on the average, below the physical standard of the former. This may be illustrated by comparing the two occupational groups of newspaper sellers and navvies etc., of Social Class V. The first occupation, which makes no demands on physique, had the very high standardized mortality ratio of 230, while the other occupation, which requires physical strength, had a ratio of only 58. The explanation of this low ratio is not that navvying is a healthy occupation but that there is a weeding out of those who become unable to do strenuous work and have to seek a lighter occupation, credited subsequently with their deaths. This process also operates between the social classes; a skilled worker would move down from Social Class III to IV or V. Conversely the average standard of health of those promoted to a higher class is probably above the mean of their original class, since indifferent health would be a handicap to promotion.

The trends of Table 1 and 2 support the suggestion that there is some relation between the growth of the social class populations and mortality. It appears that the large access of recruits to Social Classes I and II up to ages 35-44, depressed the mortality of these classes. The death rates in the age group 35-44 for the two highest social classes varied from ⅔ to ¾ of the rates of the two lowest classes. Social Class II experienced a lighter mortality than Class III from age 20 to 54, but afterwards their positions were reversed. This change occurred at the same time as the increase in the relative populations of Classes IV and V, while the population in Class III continued to decline. Promotion to the higher classes was negligible at this age so that the lower classes expanded at the expense of Class III. This factor, the removal from Class III of those whose health caused them to seek lighter occupations, may account for the lower rate in Class III than in Class II. On this hypothesis the death rates of Classes IV and V are adversely affected, up to middle life, by the promotion to higher grades of those whose physique is possibly above average, and from late middle life by the addition from the higher social classes of those whose health had deteriorated. The continued decrease, throughout life, of the relative population in Class III probably affected the mortality in two ways, adversely up to middle age, and in later life caused some retardation in the rate.

TABLE 3

Regions of England and Wales: 1930-1932

REGION	PROPORTION PER 1000 OF THE POPULATION AGED 20-65 IN SOCIAL CLASSES						STANDARDIZED MORTALITY RATIO AGES 20-65 IN SOCIAL CLASSES					
	I	II	III	IV	V	Unoccupied	I	II	III	IV	V	Unoccupied
Greater London	34	137	532	111	170	16	91	90	95	115	113	131
Remainder of South-east	37	148	475	162	157	21	91	85	82	88	88	123
North I	16	94	478	238	165	9	94	101	101	107	122	219
North II	21	168	394	197	209	10	81	86	97	101	118	161
North III	16	125	496	209	142	12	78	104	104	107	115	138
North IV	19	129	484	166	190	11	93	106	108	117	135	135
Midland I	18	132	496	180	163	12	82	96	98	106	111	131
Midland II	16	132	518	200	125	9	76	91	91	89	97	139
East	20	170	369	263	160	18	83	86	79	75	82	148
South-west	30	183	438	183	148	18	99	85	89	86	99	117
Wales I	18	114	491	227	138	11	112	107	111	108	111	181
Wales II	26	238	369	214	133	19	104	95	100	98	101	150
England and Wales	24	138	488	176	163	14	90	94	97	102	111	135

REGIONS

The proportion in each social class and the standardized mortality ratio, for ages 20-65, for the regions of England and Wales are shown in Table 3. The proportional distribution of the social classes differs considerably among the regions due to the location of the principal industries and to the variations in the social class distribution of different occupations. Social Class I was proportionately more important in the southern regions than in the northern since the Government and many large commercial undertakings had their executive and administrative staffs in London. In addition, 80 per cent of the commissioned officers of the defense forces were enumerated in the South-east and South-west regions. The regions of North II, East, South-west and Wales II had the largest proportion of Social Class II and a high proportion of Social Class IV. These regions had the largest number of agricultural workers and the classification of these workers influenced the size of these two social classes in these areas. Agricultural workers are distributed among Social Classes II to V and for the whole country the percentages in these classes were 28.4, 21.9, 44.9 and 4.9 respectively. The agricultural workers alloted to Social Class II, in the four regions, formed 6.3, 6.5, 7.4 and 13.4 per cent, respectively, of the occupied males aged 14 and upwards against 2.4 per cent for England and Wales, and the percentages of agricultural workers in Class IV were 7.2, 18.2, 9.1 and 9.8 compared with 3.8 for the whole country. The regions in which were situated the principal coalfields, North I, North III, Midlands II, Wales I, had a large proportion in Social Class IV, due to the social class classification of coal miners which was restricted to practically two groups. The percentage distribution of coal miners for the whole country was 0.4 in Class II, 53.2 in Class III, and 46.4 in Class IV. In the above four regions the coal miners in Class IV formed 14.4, 6.7, 6.2 and 12.9 per cent of the total occupied males aged 14 and upwards as compared with 3.1 per cent for the whole country. The largest proportions of Social Class V were found in the North II and North IV regions. These areas had a larger proportion of the occupied population described as general laborers, laborers and unskilled workers (class of work not specified) than in the country as a whole, the percentages being 12.1 and 12.7 compared with 9.7 for England and Wales. Internal migration affects any attempts to compare the change

in the proportional distribution of the social classes with age. The southern section of the country has become more industrialized and has attracted workers from other regions. During the decade 1921-1931 the population of the South-eastern region increased by 9.8 per cent compared with 5.5 per cent for the whole country. Midland I and II, with increases of 6.3 and 7.9 per cent, were the only other regions with a rate of increase greater than that of the whole country. In Wales I and II the population decreased by 2.2 and 2.9 per cent.

The standardized mortality ratios fluctuated considerably between the regions, and within the regions the relative position of the social class mortality varied. The negative relation between mortality and social class shown by the whole country appeared only in the regions of the North and Midland I. The chief exceptions to the trend of increasing mortality with descending social class were: Wales II where the rates for Social Class I were greater than those for Classes II to V, the remainder of the South-east region where Class III had the lowest mortality ratio, the Eastern region with the lowest ratio in Class IV, and the South-west region. The latter two regions had a large proportion of the male population engaged on the land and one third of all agricultural workers in Class IV were enumerated in these regions. The highest death rates in Social Class V were those of the four northern regions; these regions had the most densely populated areas in the country. The percentage living more than two to a room was 20.15, 7.05, 7.49 and 6.48 for North I to IV. The correlation is, however, not perfect since the death rates were not in the same order as the overcrowding index and also Greater London with an index of 9.43 had a mortality below that of the northern region.

URBANIZATION

As would be expected from the construction of the social classes, the proportional distribution of each class varies with the degree of urbanization. These distributions and the standardized mortality ratios are shown in Table 4 for the county boroughs, urban districts and rural districts outside Greater London.

The proportion of the population in Class I did not vary between the three density areas. The county boroughs had the largest proportion of Class V and the smallest proportions in Class II and IV. In the urban districts Social Class III was relatively more numerous than

TABLE 4

Areas outside Greater London: 1930-1932

AREA	SOCIAL CLASS					
	I	II	III	IV	V	Unoccupied
	Proportion per 1,000, aged 20-65					
County boroughs*	20	120	502	159	188	12
Urban districts	24	126	503	182	151	14
Rural districts	22	187	384	260	131	16
	Standardized mortality ratio, ages 20-65					
County boroughs	92	107	107	123	129	158
Urban districts	89	97	94	100	104	128
Rural districts	89	80	83	79	81	125

* In spite of a few exceptions, e. g. such ancient cities as Canterbury, the county boroughs are great towns. Rural districts are sometimes densely populated but on the average much less so than urban districts.

in the other areas. The rural districts had the largest proportions in Classes II and IV, the lowest proportions in Classes III and V, and relatively the largest number of unoccupied males. The standardized mortality ratio was negatively correlated with social class in the county boroughs and in the urban districts, although the ratio for Social Class II in the county boroughs was high and the position of Class II and III interchanged in the urban districts. The social class contrast was greatest in the county boroughs where the difference between the highest and lowest standardized mortality ratio of the five social classes was 37, compared with 15 for the urban districts and 10 for the rural districts. The standardized mortality ratios of Social Class I were practically constant in the three density areas but there was a large positive correlation between urbanization and the standardized mortality ratio in the other four social classes. The standardized mortality ratio for Social Classes II and III was approximately one third greater for county boroughs than for rural districts, while the ratio for Social Classes IV and V was almost 60 per cent larger. The increase in the ratio between rural districts and urban districts was practically the same as between urban districts and county boroughs in each of the Social Classes II to V. Occupational differences are

probably the explanation of the apparently paradoxical sequence in the social class mortality rates in the rural districts. Some of the occupations of Social Class I, with a standardized mortality ratio below the average, are probably mainly confined to urban areas; e. g. bank and insurance officials (standardized mortality ratio, 66) and professional engineers (standardized mortality ratio, 84), while medical practitioners, with a high standardized mortality ratio of 106 compared with 90 for the whole of Social Class I, possibly form a more important proportion of this social class in the rural districts than in the other areas. The areal differentiation of occupations may account for the failure of the mortality of Social Class I in the rural areas to show any improvement on the rate for the urban districts, although it is not possible to examine this point in detail. Agricultural workers influence the mortality trend of Social Classes II to IV. Almost half of this occupational group are placed in Class IV and the very low standardized mortality ratio of 79 for this class in the rural districts was due to the experience of agricultural laborers. In the rural districts one male in six was described as an agricultural laborer and one quarter of all rural males were placed in Class IV; thus about one third of this social class in the rural districts were agricultural laborers. This occupation had a standardized mortality ratio of 75 compared with an average of 102 for the whole of Social Class IV. Several of the numerically important occupations in Class IV with a mortality in excess of the average are found mainly in urban areas, e. g. workers in the textile industries, steel works, gas works, etc.

SUMMARY

The correlation between mortality and social classification is a feature of the life of large towns, and the relationship is less clearly shown by the small towns and not at all by the rural districts. The distribution of social class mortality in the regions varied considerably from the trend for the whole country. To some extent this was possibly due to the location of the larger industries and the consequent variations in the occupations and of social grading in different regions. A different occupational structure is also the most probable explanation of the different trend exhibited by the social class mortality of the rural districts from either that of the county boroughs or urban

districts. Since social class depends upon occupation, a part of the difference in the social class mortality is due to selection, some occupations demanding a certain standard of physique, but the importance of this factor is speculative.

CONTRIBUTION TO THE ANALYSIS OF THE EXCEPTIONS TO BERNSTEIN'S THEORY

BY VÁCLAV MYSLIVEC, Sc. D.

BERNSTEIN'S theory of triple allelomorphs is generally accepted as a reliable explanation of the mechanism of human blood-group inheritance. All former genetical theories such as the one proposed by Von Dungern and Hirszfeld and the theory suggested by Kirihara and Haku or the theory of Bauer are now considered to be entirely wrong because there is no evidence whatever which could support them.

Bernstein's theory, on the contrary, is rightly considered to be in full accordance with all practical observations. Furthermore, Bernstein's difference $1 - (p+q+r)$ is commonly used as a reliable criterion of homogeneity of the studied population. Exceptions which have been found are considered to be only a result of inaccurate serological technique or of illegitimacy, but no importance is given to them.

However, in our paper on homogeneity and heterogeneity of human population, which was published under the title "A contribution to the study of human blood groups" in the *Journal of Royal Anthropological Institute, of Great Britain and Ireland,* Vol. 71, Parts I and II, 1941, we came to the conclusion that Bernstein's difference $1 - (p+q+r)$ cannot be used as a reliable criterion of homogeneity of the population in question. It has been found that Bernstein's differences are not entirely independent values following the law of normal distribution as would be desired according to theory. On the contrary, it has been found that these differences are in close correlation with relative frequencies of blood group AB. Highly significant values of correlation coefficients were found in nearly all the investigated populations. Furthermore, values of the correlation coefficients are quite independent of the size of the samples. A suggestion was made, therefore, that the value of the correlation coefficient, and especially the gradient of the regression line, may be used advantageously as a criterion of homogeneity, if necessary. In the same paper it was shown that Bernstein's differences cannot be explained as a simple result of inaccurate serological

technique presumably due to interchange between blood groups A and AB or B and AB. On the other hand, it has been found that Bernstein's differences are explainable only as a result of interchange between blood groups O and AB. That was the reason why we concluded that some common element, both in the blood group O and blood group AB, may be rightly presumed. We have arrived at this conclusion by means of a statistical investigation, but we should like to mention in this connection that L. Hirszfeld and Z. Kostuch[1], as well as Thomsen[2], had previously expressed the same opinion, especially with regard to blood group O.

In the paper which we herewith submit, we are trying to investigate whether exceptions to Bernstein's theory are entirely without meaning or whether they may be of interest for us. We do not, of course, intend to challenge the validity of Bernstein's theory, but we feel that even fundamental theories, as Bernstein's theory surely is, sometimes may need certain small modifications. Nevertheless, it seems to us that both theories, Bernstein's as well as Hirszfeld's, undoubtedly may be logically connected in one complete system, while basic frames of both of them are retained. Such a step may not only be interesting from a purely theoretical point of view, but it could also help us to explain those exceptions, which are otherwise rightly or erroneously inexplicable. We are, of course, inclined to consider exceptions against any commonly accepted theory just simply as errors. But how many times have such "errors," even the smallest, subsequently proved to be right and showed us that something was really behind them? The history of science shows us many examples.

The same may or may not be true in the case of exceptions to Bernstein's theory. These exceptions may have some meaning for us or they may remain "puncture-proof errors," as they were considered before. Similarly, the theory itself may need some modification or it may remain absolutely unshakable. We may cherish a hope that we have come nearer to the truth, although it is possible we may be entirely wrong. But it matters little at which conclusion we arrive as long as we are just searching for the truth.

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[1] L. Hirszfeld and Z. Kostuch: Investigation on the blood groups with special regard to the composition of the blood group O. *Polska gazeta lekarska* (Polish Journal of Medicine), N. 36, XVII.

[2] Thomsen. *Acta Soc. Medic.* A 15, No. 9, 1932.

The summary of studies on the inheritance of blood groups, for instance the table compiled by Lattes and enlarged by the addition of the data of Shipton, Moureau, Matta, Mustakallio, and Hyman (W. C. Boyd's[3] "Blood Groups," pp. 136 and 137) shows (see Table 1) that exceptions to Bernstein's theory of triple allelomorphs are not

TABLE 1

Summary of studies on the inheritance of the blood groups

(Compiled by Lattes and enlarged by the addition of the data of Shipton, Moureau, Matta, Mustakallio and Hyman. See W. C. Boyd's "Blood Groups," pp. 136-137.)

MATING	NUMBER OF FAMILIES	NUMBER OF CHILDREN IN GROUP				
		O	A	B	AB	Total
O × O	1300	2935	**16***	**2**	0	2953
A × A	1356	519	2595	**1**	**1**	3116
O × A	2731	2463	3318	**18**	**9**	5808
B × B	298	130	0	544	**1**	675
O × B	1046	1037	**11**	1292	**1**	2341
A × B	1146	416	826	671	621	2534
O × AB	483	**40**	598	544	**34**	1216
A × AB	495	**21**	548	261	321	1151
B × AB	333	**13**	125	307	162	607
AB × AB	70	0	43	42	76	161
Total	9258	7574	8080	3682	1226	20562

* Exceptions to Bernstein's theory are in bold face type.

[3] William C. Boyd: Blood Groups. Mitgenerij W. Junk, *Den Haag*, 1939.

entirely without system. It may be seen that exceptions (numbers in bold face type) in matings A × A, and B × B are, in fact, very rare. On the contrary, matings O × O, O × A, O × B, O × AB, A × AB, and B x AB show these exceptions considerably more frequently. Though we may be inclined to believe or disbelieve that such exceptions are due to inaccurate serological technique or to illegitimacy, nevertheless the fact remains that these exceptions have generally been found in matings where at least one parent belonged to blood group O or blood group AB. W. C. Boyd and other authors have expressed the opinion that all these exceptions are due either to errors in serological technique or to illegitimacy. It is apparent, however, that the exceptions observed in the period 1935-1937, though far less frequent than before, still are 3.7 per 1000 families or 2.0 per 1000 children. What judgment on these exceptions may be actually made? Are we inclined to say that serological errors or illegitimacy were present only in certain matings while in others they were absent? As a matter of fact, D. Matta[4] has clearly shown that not all these exceptions can be explained simply as a result of illegitimacy. Furthermore, we could dare to ask the question whether all observations, which so beautifully fit Bernstein's theory, are correct after all. This question, though it seems to be curious and strange, has nevertheless quite concrete meaning. It may be rightly presumed that errors sometimes occur simply because we are inclined to consider the results of uncertain testing to be in full agreement with commonly accepted theory. By this statement we do not mean to underestimate results obtained by numerous scientific workers in this field. Nevertheless the history of science shows us many examples where exceptions to a certain commonly accepted theory became more frequent after some particular interest has been attached to them. It is true that not many exceptions were found in critical matings, but the question arises whether these exceptions should not be more frequent in reality.

In this connection it is apropos to mention that results obtained from mating A × B also may be of particular importance in this respect. Since children of any group can occur here, according to Bernstein's theory, little attention has been paid to this mating. The analysis of results obtained from this mating, however, furnishes us an important criterion of reliability as far as accuracy of testing is concerned.

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[4] Publication No. 11, Faculty of Medicine of the Egyptian University, 1937.

According to Bernstein's theory the matings A × B are of four varieties:[5]

GENOTYPES OF PARENTS	PERCENTAGE DISTRIBUTION OF GROUPS IN CHILDREN			
	O	A	B	AB
AA × BB	—	—	—	100
AA × BO	—	50	—	50
AO × BB	—	—	50	50
AO × BO	25	25	25	25

It is obvious that $(AB-O) \geqq (A-O) + (B-O)$, or in Wiener's words, the excess of group AB over group O among children should be slightly greater than the sum of excess of A over O and of B over O.

Furthermore, if the relative frequencies of genes in the population are known, then the relative frequencies of groups in children resulting from mating A × B can be easily calculated in terms of r, p, and q according to F. Schiff[6] as follows:

GROUPS OF PARENTS	BLOOD GROUPS OF CHILDREN			
	O	A	B	AB
A × B	$2pqr^2$	$2pqr(p+r)$	$2pqr(q+r)$	$2pq(p+r)(q+r)$

Thus the above-mentioned inequality

$$(AB-O) \geqq (A-O) + (B-O)$$

can be written in terms of frequencies of genes as

$$2pq(p+r)(q+r) - 2pqr^2 \geqq 2pqr(p+r) - 2pqr^2 + 2pqr(q+r) - 2pqr^2,$$

or simply

$$2pqr(p+q) + 2p^2q^2 > 2pqr(p+q).$$

[5] See Alexander S. Wiener: Blood Groups and Blood Transfusion. P. 191, Charles C. Thomas, *Springfield, Illinois*, 1943.

[6] F. Schiff: Technik der Blutgruppenuntersuchungen. P. 68, Julius Springer, *Berlin*, 1932.

This inequality shows that the excess of blood group AB over group O among the children resulting from mating A × B *always must be greater* than the sum of the excesses of blood group A over O and of B over O. Furthermore, it is easy to show that relative frequencies of blood groups in children resulting from mating should fulfill the necessary theoretical condition as follows:

$$O \times AB = A \times B,$$

or:

$$\frac{A \times B}{O \times AB} = 1.$$

How far this important condition has been fulfilled is seen from Wiener's table[7] (see Table 2) to which were added calculated values of the ratio $\frac{A \times B}{O \times AB}$. From this table it is apparent that in nearly all cases this condition was not fulfilled at all. Particularly large discrepancies are obvious in earlier reports with the exception of the pooled results of Snyder, Schiff and Thomsen. Unfortunately these pooled results are based on the lowest number of families investigated. Buining's data, obtained in 1932 from 336 investigated families, give the best results. Pooled results from the last period, 1932-1942, however, show a discrepancy although these reports are based on a large number of families (158). It is also significant that the deviations in all cases are in the same direction, pointing to the occurrence of similar technical errors.

It is of interest to mention that Bernstein, in his original paper, also used the ratio $\frac{A \times B}{O \times AB}$ in order to disprove the former theory of Von Dungern and Hirszfeld. According to that theory, ratio $\frac{A \times B}{O \times AB}$, calculated from relative frequencies of blood groups of given population, should be equal to unity. Bernstein rightly pointed out, however, that in the vast majority of populations studied thus far this relation does not hold. For this reason, the theory that the agglutinogens A and B are inherited independently of one another was not tenable.

[7] *Ibid.*, p. 191.

TABLE 2

TABLE 2

Statistical analysis of mating $A \times B$ in published studies on the heredity of the blood groups

YEARS OF STUDIES	INVESTIGATORS	NUMBER OF FAMILIES	NUMBER OF CHILDREN				(AB—O)	(A—O) + (B—O)	$\frac{A \times B}{O \times AB}$	$\left(\frac{A \times B}{O \times AB} - 1\right)$
			O	A	B	AB				
1910-1924	11 reports	92	26	64	62	38	12	74	4.016	3.016
1926-1927	Japanese authors	87	27	71	54	64	37	71	2.219	1.219
1926	Bessiedin	47	10	42	42	22	12	64	8.018	7.018
1925-1927	Furuhata, Ichida and Kishi	257	125	190	140	146	21	80	1.458	0.458
1925-1927	Snyder, Schiff and Thomsen (pooled data)	49	24	39	37	53	29	28	1.134	0.134
1925-1927	11 reports	196	50	146	103	82	32	149	3.668	2.668
1928-1929	13 reports	425	150	295	226	305	155	221	1.457	0.451
1930-1932	19 reports	198	78	119	91	82	4	54	1.693	0.693
1932	Buining	336	225	285	274	338	113	109	1.027	0.027
1932-1942	13 reports	158	74	118	96	131	57	66	1.169	0.169
	Total	1845	789	1369	1125	1261	472	916	1.548	0.548

In our case, however, we do not want to use the ratio calculated for frequencies of blood groups of children resulting from mating A × B in order to discredit the validity of Bernstein's theory. Nevertheless, this ratio can be advantageously used as a reliable criterion of accuracy of results which have been reported by scientific workers in this field.

The result of our analysis is rather disappointing with regard to the accuracy of serological technique as applied by the majority of research workers who investigated blood groups of children resulting from mating A × B. We can follow the same line of thought and ask the pertinent question whether the reported results also obtained from other matings [O × O, O × B, O × AB, A × A, A × AB, B × B, B × AB, and AB × AB] are as reliable as they are considered to be, or whether they are similarly incorrect. It is apparent that two possibilities can be considered with regard to the exceptions to Bernstein's theory. These are either that these exceptions are due to inaccuracy of testing or that the low frequencies of these exceptions, as they were reported up to now, are equally due to inaccuracy. The latter possibility, of course, means that exceptions to Bernstein's theory in critical matings might be more frequent if more correct technique were applied. Let us therefore presume in our investigation that reported exceptions to Bernstein's theory really exist but that their low frequencies, especially in some cases, are in fact due to inaccuracy of serological technique. There is no reason why we cannot use the same sort of argument which was generally used to discredit the simple existence of exceptions to Bernstein's theory.

Bernstein's theory, however, cannot give an explanation of the exceptions. On the other hand, it would be quite superfluous to propose a new theory concerned with the inheritance of blood groups in man. It is always preferable to explain exceptions to a generally accepted theory and new findings in coincidence with this reliable theory than to propose a more complicated and far more unreliable hypothesis. Nevertheless, keeping this guidance in mind, we must admit that generally accepted theories sometimes need a small modification, while the basic frames of the theory are retained.

The simplest way in which our findings may be explained is by the presence of two genes, A and B, which are closely but not completely linked. In this case, of course, we must presume that both these genes, being simultaneously on the same chromosome, are in their effect entirely eliminated and the result is blood group O. On the other hand, when

they are located in different chromosomes, though of the same pair, their action is quite independent of each other. Such a hypothesis is not as strange as it seems to be, for we must bear in mind the antagonistic effect of the elements A and B. Moreover, blood contains not only agglutinogens and agglutinins, but also haemolysines which are also specific. As a matter of fact, we do not know very much about the chemistry of these elements. We have on hand only the results of their serological effects. Very likely they might be compared to stereo-isomeres of the same organic molecules as was suggested by W. E. Castle[8] in his studies on the inheritance of blood groups in rabbits. Such a suggestion seems to be valuable for it may be quite conceivable that the arrangement of two different stereo-isomeres of the same organic molecules may manifest quite different effects depending whether they are located closely in the same chromosome or whether they are present in different chromosomes, though of the same pair. In this way a simple explanation of presumed position effects of the genes A and B and their particular manifestation in the developed morphological characters of human blood may be found. Furthermore, it may be supposed that these genetical substances could be molecules of proteins, as was anticipated long ago by Timoteff Ressowski. Taking into account such a possibility, we could suppose that the acid portions of amino acids have chemical attraction for the basic portions of others. It is known that amino acids, components of proteins, are acid in one part and basic in another, and according to the circumstances may act quite differently, either as an acid or as a base. Such a comparison is, of course, very arbitrary. Nevertheless, it may help to explain the assumed position effect.

Many analogous examples, regarding position effect of the genes, may be cited in this connection. For instance, it is well known that in *Drosophila,* two bar alleles, being located in the same chromosome, reduce the number of facets in comparison with the resulting number if they are in both homologous chromosomes.

Finally, it is necessary to point out in this connection that more recent studies on blood groups have revealed that the dominance of the genes A and B over gene R is not equal as should be presumed in accordance with Bernstein's theory. For instance, Thomsen has found

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[8] W. E. Castle: Mammalian Genetics, Harvard University Press, *Cambridge.* 1940, p. 92.

that the sensibility of agglutinogen A is diminishing in blood group AB, indicating some dominance of gene B over gene A. Similarly, it may be supposed that in particular genotypes both of the genes A and B are mutually affected, with the manifested result that neither agglutinogen A nor B is developed. Such a complete mutual recessiveness may be due to the closest localization of the genes in the same chromosome (position effect). On the other hand, if these genes are located in different chromosomes, though of the same homologous pair, then complete independence of each other may be presumed. In such a particular case, of course, both of the agglutinogens are fully developed —which means blood group AB.

If such a transitory mutual recessiveness is presumed on the one hand, and complete independence on the other, then the genetical system of blood groups O, A, B, and AB may be derived, as given in Table 3.

There it will be seen that the suggested modification, compared with Bernstein's original theory, reveals differences in the blood groups O, A, and B, where three genotypic formulae in each group are postulated. Blood group AB, however, is supposed to be a manifestation of only one genotype as in Bernstein's theory. In view of the above-mentioned position effect, it must also be pointed out that the genotypic formulae of the blood groups O, A, and B may be reduced into terms analogous with Bernstein's theory, because of the presupposed equality of chromosomes $\left[\ \right]$ and $\left[\begin{matrix}A\\B\end{matrix}\right]$.

Of particular importance is the fact, that it may be reasonable to expect crossing-over in one of the genotypes of blood group O (i. e. genotypic formula $\left[\ \right]\left[\begin{matrix}A\\B\end{matrix}\right]$) and simultaneously in the genotype of blood group AB ($\left[\begin{matrix}A\\\ \end{matrix}\right]\left[\begin{matrix}\ \\B\end{matrix}\right]$).

Taking into account the possibility of crossing-over in these genotypes, the rare exceptions to Bernstein's theory may be explained simply as cross-overs. The occurrence of these crossing-over cases is expected to be infrequent, however, because of the presumed close localization of the genes A and B with each other. It will be shown later that a very minute linkage value, 0.04-0.05, may satisfactorily explain observed exceptions to Bernstein's theory.

In the light of the foregoing discussion, it is well to emphasize again that these exceptions were mostly found in the matings, where at least one of the parents belonged to blood group O or AB. This gives a more concrete touch to the supposed possibility, for only the above-mentioned genotypes [ ][A/B] and [A][B] of the blood groups O and AB

TABLE 3

Frequencies of the four blood groups

blood groups	genotypes frequencies			Bernstein's theory:		
O	[ ][ ]	a^2	$(a+b)^2$	[R][R]	r^2	
	[ ][A/B]	$2ab$				
	[A/B][A/B]	b^2				
A	[A][A]	c^2	$c^2+2c(a+b)$	[A][A]	p^2	p^2+2pr
	[A][ ]	$2ca$		[A][R]	$2pr$	
	[A][A/B]	$2cb$				
B	[B][B]	d^2	$d^2+2d(a+b)$	[B][B]	q^2	q^2+2qr
	[B][ ]	$2da$		[B][R]	$2qr$	
	[B][A/B]	$2db$				
AB	[A][B]	$2cd$		[A][B]	$2pq$	

respectively may be considered as a material basis for crossing-over. Such a system will practically coincide with Bernstein's theory from the statistical point of view. Moreover, it also explains some facts still remaining unsolved as mentioned by D. Matta. In fact, several supplementary theories suggested in order to explain exceptions to Bernstein's theory of triple allelomorphs (by Kirihara and Haku, Furuhata and Bauer, by Ffoulkes and Eltherington, and by others), may be generally connected in this way with the accepted Bernstein theory. However, our system offers more generalization.

Let us first consider the differences, or, on the other hand, the coincidence of this system and Bernstein's theory. According to his theory, there is only one locus for the genes determining the blood groups in a single pair of chromosomes, at which locus only one of the three genes may be situated. Furthermore, according to his theory, genes A and B are both dominant over R. Since the agglutinogens A and B are inherited as Mendelian dominants, they cannot appear in the blood of a child unless present in the blood of one or both parents. When a second law of heredity is taken into account, it is obvious that no children of blood group O could be obtained from matings where one of the parents, or both, belong to blood group AB.

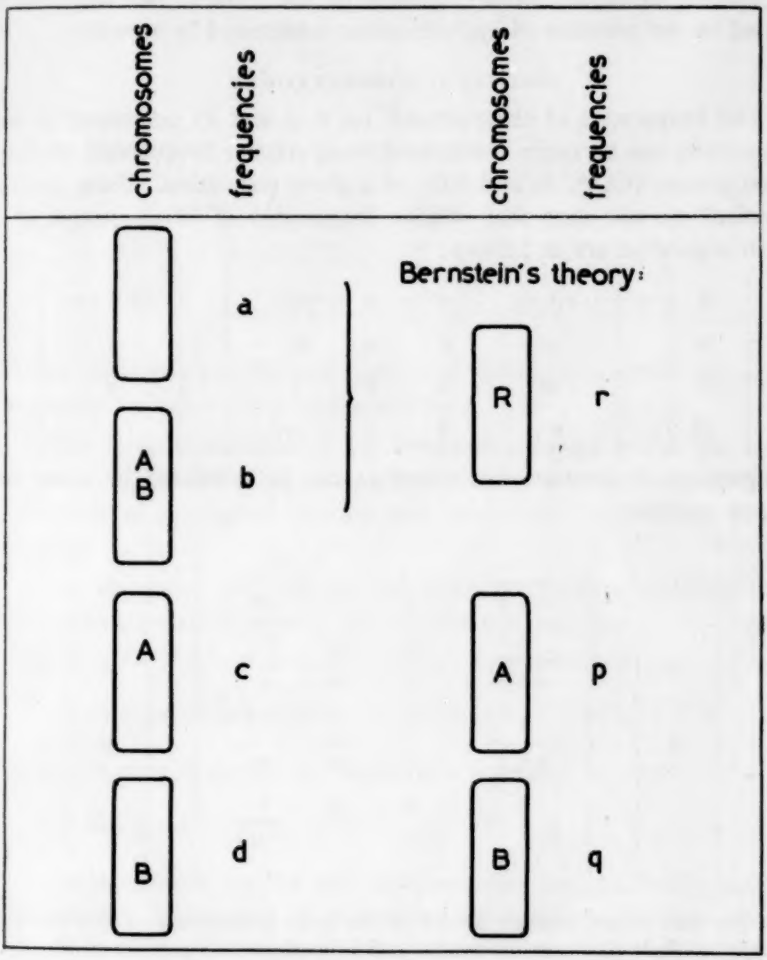
In contrast to Bernstein's theory, we assume that chromosomes, carrying only genes R, may be of two sorts, one containing neither of the genes, and the other containing both of them, as shown in Table 4. In the latter case, owing to the so-called *position effect,* the genes A and B, being simultaneously on the same chomosome, are in their manifestation mutually eliminated. Thus the two types of chromosomes are equal in their effect. For this reason there is no particular difference between this system and Bernstein's theory from the statistical point of view. However, the exceptions, still to be accounted for, may be explained by the possibility of crossing-over. This seems to be a small contribution to the forensic medicine where, until now, we find that exceptions, though nearly insignificant, are still considered. It is necessary to mention in this connection that the possibility of crossing-over was suggested by Kirihara and Haku, and by Bauer. Nevertheless, L. Snyder clearly showed that statistical observations regarding the condition of equilibrium do not support their view. However, if we keep in mind the proposed position effect of genes A and B, it is obvious that the condition for equilibrium in the population is presumably fulfilled, if such a population is also in equilibrium with the Bernstein theory. Furthermore, the link-

age value of genes A and B, suggested by Bauer to be 0.10 — 0.11, is far from correct, as will be shown later on.

Thus far we have considered the hereditary determination of the blood groups only with reference to the agglutinogens. The agglutinins have not been taken into account. The agglutinins, however, are merely correlated structures dependent for their presence upon the absence

TABLE 4

Diagram illustrating different types of chromosomes



of related agglutinogens to absorb them. Numerous studies on mothers and their new-born children have shown that agglutinogens are detectable most often just after birth, in many cases after the first few months in fetus. On the contrary, agglutinins develop considerably later. For instance, it has been shown that only about one half of new-born children have clearly demonstrable agglutinins. Furthermore, agglutinins of new-born children are obviously those of the mother. At least the child never has an agglutinin which may be capable of acting on the mother's agglutinogens. Later on in an astonishing way these improper agglutinins disappear, being replaced by the child's own agglutinins caused by the presence of agglutinogens, determined by heredity.

STATISTICAL CONSIDERATIONS

The frequencies of chromosomes (a, b, c, and d) postulated in our assumption can be easily determined from relative frequencies of four blood groups (O, A, B, and AB) of a given population. Using matrix notation[9] we can state that relative frequencies of blood groups of a given population are as follows:

$$\begin{vmatrix} \mathrm{O} \\ \mathrm{A} \\ \mathrm{B} \\ \mathrm{AB} \end{vmatrix} = \begin{vmatrix} (a+b) & 0 & 0 & 0 \\ 2c & c & 0 & 0 \\ 2d & 0 & d & 0 \\ 0 & 0 & 0 & 2cd \end{vmatrix} \cdot \begin{vmatrix} (a+b) \\ c \\ d \\ 1 \end{vmatrix}$$

Frequencies of chromosomes therefore can be calculated by using the inverse matrix:

$$\begin{vmatrix} a+b \\ c \\ d \\ 1 \end{vmatrix} = \begin{vmatrix} \frac{1}{a+b} & 0 & 0 & 0 \\ -\frac{2}{a+b} & \frac{1}{c} & 0 & 0 \\ \frac{2}{a+b} & 0 & \frac{1}{d} & 0 \\ 0 & 0 & 0 & \frac{1}{2cd} \end{vmatrix} \cdot \begin{vmatrix} \mathrm{O} \\ \mathrm{A} \\ \mathrm{B} \\ \mathrm{AB} \end{vmatrix}$$

[9] We used matrix notation instead of the usual development of $(a+b+c+d)$ in order to show that matrices can be used in mathematical genetics.

Multiplying the inverse matrix on the right side of this equation by the column matrix we obtain the following system of equations:

$$(a+b) = \frac{O}{(a+b)},$$

$$c = -\frac{2O}{(a+b)} + \frac{A}{c},$$

$$d = \frac{2O}{(a+b)} + \frac{B}{d},$$

$$1 = \frac{AB}{2cd}.$$

From these questions it is obvious that:

$$(a+b) = \sqrt{O}$$

$$c = \sqrt{O+A} - \sqrt{O}, \text{ or } c = 1 - \sqrt{O+B}$$

$$d = \sqrt{O+B} - \sqrt{O}, \text{ or } d = 1 - \sqrt{O+A}.$$

These equations are the two systems of Bernstein's equations, where r is replaced by $(a+b)$, p by c, and q by d.

The theoretical condition for Bernstein's theory is that the sum of $(r+p+q)$ should be equal to unity. The same condition must be fulfilled also in our case so that the sum $(a+b+c+d)$ should be equal to unity.

The deviation (D) of the calculated frequencies of chromosomes from the theoretical value is numerically the same but of opposite sign according to which system of Bernstein's equations is used:

$$D = 1 - (a+b+c+d) = 1 + \sqrt{O} - \sqrt{O+A} - \sqrt{O+B},$$

or if the second system of Bernstein's equations is used:

$$1 - (a+b+c+d) = \sqrt{O+A} + \sqrt{O+B} - \sqrt{O} - 1 = -D.$$

Since selective mating and also mutation are practically excluded, the relative frequencies of respective chromosomes and also of genes should remain constant from one generation to another. Furthermore,

if crossing-over is presumed, the following condition of equilibrium must be fulfilled:

$$a \cdot b = c \cdot d,$$

where a, b, c, and d are relative frequencies of the respective chromosomes $\left[\ \right]$, $\left[\begin{matrix}\mathrm{A}\\ \mathrm{B}\end{matrix}\right]$, $\left[\mathrm{A}\right]$, and $\left[\mathrm{B}\right]$.

From the equations:

$$a + b = \sqrt{\mathrm{O}}$$
$$a \cdot b = c \cdot d$$

it is obvious that:

$$a \cdot b = \tfrac{1}{2}\,[\sqrt{\mathrm{O}} + \sqrt{(\mathrm{O} - 4cd)}] \cdot \tfrac{1}{2}\,[\sqrt{\mathrm{O}} - \sqrt{(\mathrm{O} - 4cd)}].$$

But $2cd$ is the relative frequency of blood group AB, so that:

$$a \cdot b = \tfrac{1}{2}\,[\sqrt{\mathrm{O}} + \sqrt{(\mathrm{O} - 2\mathrm{AB})}] \cdot \tfrac{1}{2}\,[\sqrt{\mathrm{O}} - \sqrt{(\mathrm{O} - 2\mathrm{AB})}]$$

and therefore:

$$a = \tfrac{1}{2}\,[\sqrt{\mathrm{O}} + \sqrt{(\mathrm{O} - 2\mathrm{AB})}],$$

and

$$b = \tfrac{1}{2}\,[\sqrt{\mathrm{O}} - \sqrt{(\mathrm{O} - 2\mathrm{AB})}].$$

For the sake of completeness, it is necessary to say that there is an ambiguity in the equations for a and b, since their values could be reversed. However, this ambiguity is quite irrelevant in our problem and if we used the reversed notation, we would arrive at the same result as far as linkage value is concerned.

From Table 5, it is seen that the process of calculating relative frequencies of chromosomes is practically the same in our system as in Bernstein's theory, the only difference being that we assume that the value of r is composed of two parts.

Frequencies of genes A and B may be estimated by applying the first probability theorem as follows:

Let p = frequency of A

q = frequency of B

$\overline{p}$ = frequency of absence of A

$\overline{q}$ = frequency of absence of B.

Then it may be written that:

$$p = b + c \qquad \overline{p} = a + d$$
$$q = b + d \qquad \overline{q} = a + c.$$

It is apparent that if the condition $a + b + c + d = 1$ is satisfactorily fulfilled, then, of course:

$$p + \overline{p} = 1, \quad q + \overline{q} = 1 \text{ and } (p + \overline{p})\ (q + \overline{q}) = 1.$$

TABLE 5

Method of calculation of chromosome frequencies

Chromosomes (our theory)	Frequencies		Chromosomes (Bernstein's theory)
[ ]	$a = \frac{1}{2}\left\{\sqrt{0} + \sqrt{(0-2AB)}\right\}$	$= \sqrt{0} = r$	[R]
[A B]	$b = \frac{1}{2}\left\{\sqrt{0} - \sqrt{(0-2AB)}\right\}$		
[A]	$c = \sqrt{(0+A)} - \sqrt{0}$, or $1 - \sqrt{(0+B)}$	$= p$	[A]
[B]	$d = \sqrt{(0+B)} - \sqrt{0}$, or $1 - \sqrt{(0+A)}$	$= q$	[B]

$$a+b+c+d = 1 = r+p+q$$
$$1-(a+b+c+d) = D = 1-(r+p+q)$$
$$D = 1+\sqrt{0}-\sqrt{(0+A)}-\sqrt{(0+B)}$$

By applying the second probability theorem we may write:

$$\left.\begin{aligned} \bar{p}\bar{q} &= a \\ pq &= b \\ p\bar{q} &= c \\ \bar{p}q &= d \end{aligned}\right\}, \text{ if the condition } ab = cd \text{ is fulfilled.}$$

It is also obvious that:

$$\left.\begin{aligned} \bar{p}\bar{q} &= (a+d)\cdot(a+c) = a + dc - ab = a \\ pq &= (b+c)\cdot(b+d) = b + cd - ab = b \\ p\bar{q} &= (b+c)\cdot(a+c) = c - cd + ab = c \\ \bar{p}q &= (a+d)\cdot(b+d) = d - cd + ab = d \end{aligned}\right\} = 1.$$

Similarly, *frequencies of the blood groups* O, A, B, and AB may be derived in terms of p, q, $\bar{p}$, and $\bar{q}$ in the following way:

$$\mathrm{O} = (\bar{p}\bar{q} + pq)^2$$

$$\mathrm{A} = (p\bar{q})^2 + 2p\bar{q}\,(\bar{p}\bar{q} + pq)$$

$$\mathrm{B} = (\bar{p}q)^2 + 2\bar{p}q\,(\bar{p}\bar{q} + pq)$$

$$\mathrm{AB} = 2p\bar{q}\cdot\bar{p}q = 2\bar{p}\bar{q}\cdot pq, \text{ if } p + \bar{p} = 1 \text{ and } q + \bar{q} = 1.$$

These possible combinations are expressed by the equation:

$$\mathrm{O+A+B+AB} = (\bar{p}\bar{q}+pq+p\bar{q}+\bar{p}q)^2 = [(p+\bar{p})\cdot(q+\bar{q})]^2 = 1;$$

which may be also written

$$\mathrm{O + A + B + AB} = (a + b + c + d)^2 = (r + p + q)^2 = 1,$$

when either frequencies of chromosomes or Bernstein's frequencies of genes R, A, and B are used.

ESTIMATION OF LINKAGE VALUE

Taking into account the assumed postion effect between genes A and B, in the case where both these are present simultaneously on the same chromosome, and the possibility of the crossing-over of chromosomes, we can estimate the linkage value of genes; which allows the determination of the linear distance between their actual positions on the chromosome. For this purpose we must first express group frequencies of children resulting from each mating in terms of relative

TABLE 6

Relative frequencies of children in each mating in terms of a, b, c, and d

Groups of parents	Blood groups of children				
	O	A	B	AB	All children
O × O	$(a+b)^4 - 4ab(a+b)^2x + 4(ab)^2x^2$	$2ab(a+b)^2x - 3(ab)^2x^2$	$2ab(a+b)^2x - 3(ab)^2x^2$	$2(ab)^2x^2$	$(a+b)^4$
O × A	$2c(a+b)^3 - 2c(a+b)2abx$	$2c(a+b+c)(a+b)^2 - 2c^2abx$	$2c(a+b)abx$	$2abc(a+b+c)x$	$4(a+b)^3c + 2(a+b)^2$
O × B	$2d(a+b)^3 - 2d(a+b)2abx$	$2d(a+b)abx$	$2d(a+b+d)(a+b)^2 - 2d^2abx$	$2abd(a+b+d)x$	$4(a+b)^3d + 2(a+b)^2$
A × A	$c^2(a+b)^2$	$c^2(a+b+c)(c+3a+3b)$			$4(a+b)^2c^2 + 4(a+b)c^3$
A × B	$2cd(a+b)$	$2cd(a+b)(a+b+c)$	$2cd(a+b)(a+b+d)$	$2cd(a+b+c)(a+b+d)$	$8(a+b)^2cd + 4(a+b)(c$ $+2c^2d^2$
B × B	$d^2(a+b)^2$		$d^2(a+b+d)(d+3a+3b)$		$4(a+b)^2d^2 + 4(a+b)d$
O × AB	$4cd(a+b)^2x - 8abcdx^2$	$2cd(a+b)^2 - 2abcdx$ $-2cd(a+b)^2x + 6abcdx^2$	$2cd(a+b)^2 - 2abcdx$ $-2cd(a+b)^2x + 6abcdx^2$	$4abcdx - 4abcdx^2$	$4(a+b)^2cd$
A × AB	$4c^2d(a+b)x$	$2c^3d + 4c^2d(a+b) + 2c^3dx$	$2c^2d(a+b) - 2c^2d(a+b)x$	$2c^2d(a+b+c) - 2c^2d(a+b+c)x$	$8(a+b)c^2d + 4c^3d$
B × AB	$4cd^2(a+b)x$	$2cd^2(a+b) - 2cd^2(a+b)x$	$2cd^3 + 4cd^2(a+b) + 2cd^3x$	$2cd^2(a+b+d) - 2cd^2(a+b+d)x$	$8(a+b)cd^2 + 4cd^3$
AB × AB	$4(cd)^2x^2$	$(cd)^2 + 2(cd)^2x - 3(cd)^2x^2$	$(cd)^2 + 2(cd)^2x - 3(cd)^2x^2$	$2(cd)^2 - 4(cd)^2x + 2(cd)^2x^2$	$4c^2d^2$
All parents	$\underbrace{(a+b)^2(a+b+c+d)^2}_{(a+b)^2}$	$\underbrace{[c^2+2c(a+b)](a+b+c+d)^2}_{c^2+2c(a+b)}$	$\underbrace{[d^2+2d(a+b)](a+b+c+d)^2}_{d^2+2d(a+b)}$	$\underbrace{2cd(a+b+c+d)^2}_{2cd}$	$(a+b+c+d)^4 =$

ups of children		
B	AB	All children
$+b)^2x-3(ab)^2x^2$	$2(ab)^2x^2$	$(a+b)^4$
$+b)abx$	$2abc(a+b+c)x$	$4(a+b)^3c+2(a+b)^2c^2$
$+d)(a+b)^2-2d^2abx$	$2abd(a+b+d)x$	$4(a+b)^3d+2(a+b)^2d^2$
		$4(a+b)^2c^2+4(a+b)c^3+c^4$
$+b)(a+b+d)$	$2cd(a+b+c)(a+b+d)$	$8(a+b)^2cd+4(a+b)(c+d)cd$ $+2c^2d^2$
$-d)(d+3a+3b)$		$4(a+b)^2d^2+4(a+b)d^3+d^4$
$)^2-2abcdx$ $b)^2x+6abcdx^2$	$4abcdx-4abcdx^2$	$4(a+b)^2cd$
$)-2c^2d(a+b)x$	$2c^2d(a+b+c)-2c^2d(a+b+c)x$	$8(a+b)c^2d+4c^3d$
$d^2(a+b)+2cd^3x$	$2cd^2(a+b+d)-2cd^2(a+b+d)x$	$8(a+b)cd^2+4cd^3$
$.d)^2x-3(cd)^2x^2$	$2(cd)^2-4(cd)^2x+2(cd)^2x^2$	$4c^2d^2$
$+b)](a+b+c+d)^2$ $2d(a+b)$	$\frac{2cd(a+b+c+d)^2}{2cd}$	$(a+b+c+d)^4=1$

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frequencies of chromosomes, and at the same time take the linkage value into consideration. We can then estimate linkage value by solving the equations in which observed relative frequencies of cross-overs (exceptions to Bernstein's theory) are placed on one side of the equations and expected relative frequencies of cross-overs on the other.

The expected frequencies of the children of respective blood groups resulting from each mating are listed in Table 6, where x denotes the crossing-over value.

This table was constructed under the assumption that the combination of chromosomes $\left[\ \right]\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$ gives not only chromosomes of types $\left[\ \right]$ and $\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$, but also chromosomes $\left[\text{A}\right]$ and $\left[\text{B}\right]$, due to crossing-over. If we consider the relative frequency of the genotype as unity, the relative frequency of the first two chromosomes resulting from the combination is $1-x$, and of the second two chromosomes, is x. Similarly the genotype $\left[\text{A}\right]\left[\text{B}\right]$ gives chromosomes $\left[\text{A}\right]$ and $\left[\text{B}\right]$, each with a relative frequency of $1-x$, and also the crossing-over chromosomes $\left[\ \right]$ and $\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$ each with a relative frequency of x, if the relative frequency of the genotype is taken as unity.

As an example, let us derive relative frequencies of all possible children which may result from mating O $\times$ O. Phenotype of blood group O under our assumption can be one of the following genotypes $\left[\ \right]\left[\ \right]$, $\left[\ \right]\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$, $\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$, occurring with the respective relative frequencies a^2, $2ab$, and b^2. The first of these gives only one type of chromosome, $\left[\ \right]$ where neither gene A nor gene B is present, and this occurs with the relative frequency $2a^2$. Similarly the third gives only one type of chromosome $\left[\begin{matrix}\text{A}\\\text{B}\end{matrix}\right]$ where both genes A and B are present, and this occurs with a relative frequency $2b^2$. The second type of

genotype, however, gives four types of chromosomes, two normal types [ ], and [A/B] each with a relative frequency $2ab\ (1-x)$ and two resulting from crossing-over, [A] and [B], each with a relative frequency $2abx$.

Thus in the case of free mating, which there is every reason to suppose really exists, if both parents belong to group O, four types of possible chromosomes come into play [ ], [A/B], [A], [B], the relative frequencies of the first being equal to $[2a^2 + 2ab\ (1-x)]$, of the second equal to $[2b^2 + 2ab\ (1-x)]$ and of each of the last two being equal to $2\ abx$. Since in the case of blood groups no sex linkage has been found or suspected to exist, it can be assumed that half of these chromosomes were of maternal origin and half of paternal origin. Therefore, the relative frequencies just given must be divided by two before we start to construct the usual chess-board scheme.

Applying these relative frequencies of given chromosomes, we can write the usual chess-board scheme for mating O × O shown in Table 7.

Taking into account the supposed position effect of mutual action and elimination between gene A and gene B, simultaneously present on the same chromosome, meaning equality of chromosomes [A/B] and [ ] regarding their phenotypical manifestation, we obtain the following relative frequencies of phenotypes of children resulting from mating O × O (see Table 8).

The relative frequencies of possible children resulting from other matings were derived in similar manner. It is assumed that the reader can easily follow this method, and therefore derivations of relative frequencies of possible children from all other matings were omitted simply for the sake of brevity.

The relative frequencies of blood groups in children resulting from each respective mating are given in Table 6. This table also contains both the relative frequencies of all possible children resulting from each

TABLE 7

Chess-board scheme for mating O × O

TABLE 7

Chess-board scheme for mating O × O

Types of chromosomes and their relative frequencies		Types of chromosomes and their relative frequencies			
		$a^2 + ab(1-x)$	$b^2 + ab(1-x)$	abx	abx
	$a^2+ab(1-x)$	blood group O $[a^2+ab(1-x)]^2$	blood group O $[a^2+ab(1-x)][b^2+ab(1-x)]$	blood group A $[a^2+ab(1-x)]abx$	blood group B $[a^2+ab(1-x)]abx$
	$b^2+ab(1-x)$	blood group O $[a^2+ab(1-x)][b^2+ab(1-x)]$	blood group O $[b^2+ab(1-x)]^2$	blood group A $[b^2+ab(1-x)]abx$	blood group B $[b^2+ab(1-x)]abx$
	abx	blood group A $[a^2+ab(1-x)]abx$	blood group A $[b^2+ab(1-x)]abx$	blood group A $[abx]^2$	blood group AB $[abx]^2$
	abx	blood group B $[a^2+ab(1-x)]abx$	blood group B $[b^2+ab(1-x)]abx$	blood group AB $[abx]^2$	blood group B $[abx]^2$

particular mating (sum of all elements in the same row) and the relative frequencies of children of the same blood group derived from all possible matings (sum of all elements in each respective column). It

TABLE 8

Relative frequencies of phenotypes resulting from mating $O \times O$

Phenotypes (blood groups of children)	Genotypical combination	Relative frequencies of genotypes
O	[ ][ ]	$[a^2 + ab(1-x)]^2$
	[ ][A B]	$2[a^2 + ab(1-x)][b^2 + ab(1-x)]$
	[A B][A B]	$[b^2 + ab(1-x)]^2$
	Total	$(a+b)^4 - 4ab(a+b)^2x + 4(ab)^2x^2$
A	[ ][A]	$2[a^2 + ab(1-x)]abx$
	[A B][A]	$2[b^2 + ab(1-x)]abx$
	[A][A]	$[abx]^2$
	Total	$2ab(a+b)^2x - 3(ab)^2x^2$
B	[ ][B]	$2[a^2 + ab(1-x)]abx$
	[A B][B]	$2[b^2 + ab(1-x)]abx$
	[B][B]	$[abx]^2$
	Total	$2ab(a+b)^2x - 3(ab)^2x^2$
AB	[A][B]	$2[abx]^2$
Total		$(a+b)^4$

is interesting to note that relative frequencies of children of the same blood group derived from all possible matings contain the invariant factor $(a + b + c + d)^2$, which is obviously equal to unity.

Therefore, the relative frequencies of the different blood groups in children, coming from all possible matings are as follows: group O,

$[a+b]^2$; group A $[c^2+2c\ (a+b)]$; group B, $[d^2+2d\ (a+b)]$; and group AB, $[2cd]$. This means that the distribution of blood groups in children, derived from all possible matings is the same as that in the parental population.

The total frequency of all possible children resulting from all possible matings is obviously equal to $(a+b+c+d)^4$, that is, equal to unity, as should be expected. For the sake of completeness it may be worth mentioning here that the sum of all columns is equal to $(a+b+c+d)^4$ if we take into account the above-mentioned invariant factor, which is equal also to $(a+b+c+d)^2$, or, in other words, equal to unity.

This table of blood group frequencies of children resulting from each mating is similar to the table given by F. Schiff[10] for Bernstein's theory of triple allelomorphs, where, however, the possibility of linkage was entirely excluded. In our table, if we replace $(a+b)$ by r, c by p, and d by q, and if linkage value is equal to zero, all the formulae given in our table become the respective items of the table constructed by F. Schiff.

Some objection may arise as to the possibility of starting our investigation with a population which is obviously composed of samples of different origin. But results of our recent study on this problem clearly show that pooled samples may satisfy the condition which has been supposed to establish the homogeneity of population. It has been shown by Morant that in the case of a particular metric character, the distribution for samples representing different racial populations may itself show close approach to a normal distribution. Our case with regard to blood groups is analogous. If a sample clearly fails to satisfy either test—Bernstein's for blood groups or a close approach to a normal distribution for other metrical characters—then it is safe to conclude that the population is racially heterogeneous. But if a sample clearly satisfies the test it is not safe to conclude that the racial homogeneity is thereby established. This is so because experience shows that samples known to represent a heterogeneous population are quite likely to satisfy the test, though some will not do so. In other words, compliance with theoretical criteria is a necessary condition, but not a sufficient and crucial one. It may also be realized that samples derived from a large community like New York may satisfy the test though these samples are in fact pooled samples, too. The same is true, though in less degree,

[10] *Ibid*, p. 68.

of samples derived from the white population of the United States. We can therefore say that our pooled sample is no less suitable for a study of blood group inheritance than are samples derived from the white population of the United States or of New York.

Besides having a pooled sample of population of parents, we also have a pooled sample of population of children. The same consideration regarding suitability can be applied here.

The observed relative frequencies of blood groups of both these samples are listed in Table 9. This table was constructed from the data

TABLE 9

Observed relative frequencies of blood groups in pooled samples of parent and of children populations

	A. POPULATION OF PARENTS		B. POPULATION OF CHILDREN	
BLOOD GROUP	Number	Relative frequency	Number	Relative frequency
O	6,860	0.370490	7,574	0.368349
A	7,084	0.382588	8,080	0.392958
B	3,121	0.168557	3,682	0.179068
AB	1,451	0.078365	1,226	0.059625
Total	18,516	1.000000	20,562	1.000000

of Table 1, where the sum of each column represents the number of children of each particular blood group in a population of children. The number of persons belonging to the respective blood groups of the parental sample was calculated as follows: if the parents belonged to the same blood group, the number of such families had to be multiplied by two to get the number of persons contributed by such families to the parental population of that blood group. If the parents belonged to different blood groups the number of families represented the number of parents to be contributed to each of the blood groups in question.

By using the relative frequencies of blood groups as those listed in Table 9, the relative frequencies of chromosomes (values *a*, *b*, *c*, and *d*) were calculated separately for the population of parents and for the population of children. By applying both systems of Bernstein's equations together with our equations for determining the

relative frequencies of *a* and of *b*, the following values of relative frequencies of chromosomes were obtained (see Table 10).

TABLE 10

Relative frequencies of chromosomes of parental population (A), and of population of children (B)

TYPES OF CHROMOSOMES	(A) POPULATION OF PARENTS		(B) POPULATION OF CHILDREN	
	Resulting from Bernstein's equations of systems			
	I	II	I	II
a	0.549496	0.544083	0.541661	0.546183
b	0.059191	0.064604	0.065216	0.060694
c	0.259126	0.265834	0.265648	0.260135
d	0.125479	0.132187	0.132988	0.127475
Difference				
$D = 1 - (a+b+c+d)$	+0.006708	−0.006708	−0.005513	+0.005513

The average values for the population of parents and for the population of children are given separately in Table 11, together with differences between the respective proportions.

TABLE 11

Average values of relative frequencies of chromosomes for parental population (A) and for population of children (B)

TYPES OF CHROMOSOMES	(A) POPULATION OF PARENTS	(B) POPULATION OF CHILDREN	DIFFERENCES BETWEEN RESPECTIVE ITEMS OF PARENTAL POPULATION AND POPULATION OF CHILDREN
a	0.546790	0.543922	+0.002868
b	0.061897	0.062955	−0.001058
c	0.262480	0.262892	−0.000412
d	0.128833	0.130231	−0.001398
Total	1.000000	1.000000	0.000000

The close coincidence of the average values, calculated for the population of parents (A), and for the population of children (B), is obvious. This may be considered to be convincing proof of the stability of the population regarding blood groups in successive generations, and furthermore, as proof of their Mendelian inheritance. Analysis of differences between respective items of population of parents and population of children shows that in some cases erroneous testing can be presumed. The relative frequencies of chromosomes in both cases are nearly equal. On the other hand, an interchange between blood group O and blood groups A and AB can be presumed, inasmuch as differences of the relative frequencies of values of a and of d are of opposite sign. It may also be noted that the difference $1 - (a+b+c+d)$ calculated for the population of children (—0.005513 or +0.005513) for the same system of Bernstein's equations is of opposite sign and smaller value in comparison with the difference obtained for population of parents (+0.006708 or —0.006708). This result could be explained if we assume that the differences $1 - (a+b+c+d)$ in successive generations are oscillating about a zero value and acquiring in successive generations smaller and smaller values, thus tending toward zero when the stable population is reached. In this damped oscillation of differences $1 - (a+b+c+d)$, an explanation may be found as to why these differences are sometimes positive and sometimes negative. Detailed investigation regarding this particular problem will be given in a separate paper.

The observed relative frequencies of blood groups in children resulting from each mating are given in Table 12. These values were calculated from the corresponding absolute numbers of children given in Table 1.

The linkage value (x) can be estimated by solving equations where the observed relative frequencies of cross-overs (exceptions to Bernstein's theory) are compared with expected relative frequencies of possible cross-overs given in terms of relative frequencies of chromosomes (values of a, b, c, and d) and in terms of linkage value. The relative frequencies of chromosomes are known, because these have been already calculated for the population of parents (see Table 11). Linkage value (x) thus can easily be found by solution of appropriate equations. For example, the observed relative frequency of exceptions of blood group B, reported in mating O × A, is 0.000875. The theoretical relative fre-

TABLE 12

Observed relative frequencies of children in each mating

GROUPS OF PARENTS	BLOOD GROUPS OF CHILDREN				
	O	A	B	AB	Total
O×O	0.142739	0.000778	0.000097	0	0.143614
O×A	0.119784	0.161366	0.000875	0.000438	0.282463
O×B	0.050433	0.000535	0.062834	0.000048	0.113850
A×A	0.025241	0.126204	0.000049	0.000049	0.151543
A×B	0.020232	0.040171	0.032633	0.030201	0.123237
B×B	0.006322	0	0.026457	0.000049	0.032828
O×AB	0.001945	0.029083	0.026457	0.001654	0.059139
A×AB	0.001021	0.026651	0.012693	0.015611	0.055976
B×AB	0.000632	0.006079	0.014930	0.007879	0.029520
AB×AB	0	0.002091	0.002043	0.003696	0.007830
Total	0.368349	0.392958	0.179068	0.059625	1.000000

quency of this cross-over according to Table 6 is given by the expression $2abc(a+b)x$. Therefore, we can write the equation

$$2abc(a+b)x = 0.000875,$$

where a, b, c, and d stand for the relative frequencies of chromosomes in parental population, which have been already estimated and where x stands for linkage value, which has to be found by the solving of this equation. In this case, we obtain the value x as 0.081. In the same way, we can also calculate linkage values according to the relative frequencies of cross-overs reported from other matings.

The observed relative frequencies of cross-overs are in fact very small, and for this reason we considered it more appropriate to calculate linkage value not separately for each cross-over, but for all cross-overs of the same mating, combined. This procedure seems to be more correct. For example, in mating O × A we have a cross-over of blood group B with the reported relative frequency 0.000875 and a cross-over of blood group AB with the relative frequency 0.000438. Thus, the sum of all cross-overs reported in this mating is equal to 0.001313. The theoretical frequency of all possible cross-overs of this mating is given by the expression $2abc\,[c+2\,(a+b)]\,x$. Thus, we can write:

$$2abc\,[c+2\,(a+b)]\,x = 0.001313.$$

By solving this equation for x we find that the linkage value in this case is equal to 0.050. In an analogous way we proceed with the calculation of linkage value, also using results from other matings. Thus, we find that mating O × O gives a linkage value of 0.018, mating O × B of 0.050, mating O × AB a value of 0.067, mating A × AB a value of 0.047, and mating B × AB a value of 0.060.

We can, however, proceed to calculate the linkage value in another way. We can calculate linkage value by using exceptions only of the same blood group but resulting from all possible matings. Both these methods were used and the results are given in Table 13. Estimated values of linkage calculated by using these two methods are given in the last column and in the bottom row of this table. These results were obtained by using all the exceptions from the same mating (values in last column) plus the exceptions of the same blood group but resulting from all matings (values in bottom row). Surprisingly, these values show very small variation though they were calculated by two independent methods. The average of all values obtained by using exceptions in rows (that is exceptions from each mating) is equal to 0.049 and the average of the values calculated by means of exceptions in columns (exceptions of the same blood group but from all matings) is also equal to 0.049. This value is also equal to the value of x calculated for all exceptions combined using the equation:

$$[2ab + 2ab(a+b)^2 + 4cd\ (a+b)]\ x - [12\ \ abcd + 4\ (ab)^2]\ x^2 = 0.008023.$$

It should be stated that nearly all the equations which have been used are quadratic. That means we obtain by their solution two roots, both of positive sign, but one greater than unity. It is obvious that only the root which is less than unity has logical meaning as a measure of linkage. The linkage values estimated for each mating separately are as follows:

Mating	*Estimated linkage value (x)*		
O × O	0.018		
O × A	0.050		
O × B	0.050	0.055	0.049
O × AB	0.067		
A × AB	0.047		
B × AB	0.060		

TABLE 13

Estimation of linkage value (x) from observed relative frequencies of exceptions

TABLE 13

Estimation of linkage value (x) from observed relative frequencies of exceptions

Groups of parents	Relative frequencies of exceptions of blood group					Average value of x
	O	A	B	AB	All blood groups	
O × O		$2ab(a+b)^2x-3(ab)^2x^2$ $=0.000778$	$2ab(a+b)^2x-3(ab)^2x^2$ $=0.000097$	$2(ab)^2x^2=0$	$4ab(a+b)^2x-4(ab)^2x^2$ $=0.000875$ $x=0.018$	$x=0.049$
O × A			$2abc(a+b)x=0.000875$	$2abc(a+b+c)x=0.000438$	$2abc[c+2(a+b)]x$ $=0.001313$ $x=0.050$	
O × B		$2abd(a+b)x=0.000537$		$2abd(a+b+d)x=0.000048$	$2abd[d+2(a+b)]x$ $=0.000583$ $x=0.050$	
O × AB	$4cd(a+b)^2x-8abcdx^2$ $=0.001945$			$4abcdx-4abcdx^2$ $=0.001654$	$4cd[ab+(a+b)^2]x$ $-12abcdx^2=0.003599$ $x=0.067$	$x=0.055$
A × AB	$4c^2d(a+b)x=0.001021$				$4c^2d(a+b)x=0.001021$ $x=0.047$	
B × AB	$4cd^2(a+b)x=0.000632$				$4cd^2(a+b)x=0.000632$ $x=0.060$	
All parents	$4cd(a+b)x-8abcdx^2$ $=0.003598$ $x=0.044$	$2ab(a+b)(a+b+d)x$ $-3(ab)^2x^2=0.001313$ $x=0.043$	$2ab(a+b)(a+b+c)x$ $-3(ab)^2x^2=0.000972$ $x=0.027$	$2ab(c+d)x-[4abcd$ $-2(ab)^2]x^2=0.00214$ $x=0.081$	$[2ab+2ab(a+b)^2+4cd(a+b)]x$ $-[12abcd+4(ab)^2]x^2=0.008023$ $x=0.049$	
Average value of x	$x=0.049$					

From this table it is apparent that the estimated linkage values are in all cases, except mating O × O, nearly numerically equal. Without the O × O mating they show a very small variation, with an average value of 0.055. We consider this average value is a more accurate estimate of the linkage value than 0.049 calculated for all matings. The linkage value calculated for mating O × O is considerably lower (0.018) than the values obtained from other matings, and we conclude that this exceptional case is due to erroneous testing of blood groups in children resulting from mating O × O, at least as far as exceptions to Bernstein's theory are concerned.

The question arises why only mating O × O gives an exceptionally small linkage value. We may answer this question by pointing out that, according to the opinion of L. Hirszfeld and Z. Kostuch[11] and similarly of Thomsen[12], the so-called agglutinin a_2 may be an agglutinin acting specially on blood O. For this reason it may be that not all children resulting from mating O × O were accurately tested. Unfortunately, statistical material regarding sub-groups A_1 and A_2 is insufficient as yet to allow proper investigation of this question.

We can also conclude that undoubtedly in some cases an interchange between blood groups B and AB occurred. This is obvious from the linkage values calculated by using exceptions of the same blood group but resulting from all matings (values in the bottom row in our table). The linkage value calculated by using exceptions of blood group O (0.044) is nearly equal to the value calculated for exceptions of blood group A (0.043). However, the linkage value calculated for exceptions of blood group B is smaller (0.027) and the value for exceptions of blood group AB, on the contrary, is larger (0.081) than the average calculated for all four blood groups (0.049). For this reason we may assume that some of the children actually of blood group B were erroneously tested and listed as blood group AB. In this connection it may be interesting to mention that A. Wiener also is of the opinion that the interchange between blood group B and blood group AB may be presumed, with the result that the frequencies of children from mating A × B do not then fulfill theoretical conditions. The discrepancy which has been found in a majority of reported results from mating A × B according to Wiener is due to this interchange between blood group

[11] *Ibid.*

[12] *Ibid.*

B and blood group AB. Wiener is inclined to believe that some children actually of blood group AB were tested as of blood group B, but our results indicate, rather, an interchange in the opposite direction. Nevertheless, our results agree with Wiener's as far as the possibility of interchange between these two blood groups is concerned.

At the conclusion we should like to say that in this paper we do not want to question the validity of Bernstein's theory or to propose a new theory instead. Our aim is only to show that both theories of blood group inheritance, the former theory of Von Dungern and Hirszfeld on the one hand, and the commonly accepted theory of Bernstein on the other hand, can be connected into one system. The linkage, as suggested in our paper, is open to discussion and even may be found not acceptable at all. Nevertheless, one point could be mentioned here. If human blood groups were really inherited by two linked genes with the value of linkage being as suggested, then not many more exceptions to Bernstein's theory could be reasonably expected than were found before. In other words, the results from matings will be practically the same. For this reason it is difficult to prove that the presumption of linkage is correct but it seems to be equally difficult to disprove it. The answer to this question undoubtedly will be found in the future if more accurate serological technique will be applied than was in the past. It may be expected that more accurate testing will not disprove exceptions to Bernstein's theory but on the contrary give them a square deal and the right to exist.

SUMMARY

1. In this paper it has been pointed out that the summary of studies on the inheritance of blood groups gives every evidence that exceptions to Bernstein's theory of triple allelomorphs are not entirely without system. In particular, these exceptions are rarely in matings A $\times$ A and B $\times$ B but comparatively more frequent in other matings, where at least one of the parents belonged either to the blood group O or to the blood group AB. That means that exceptions follow a definite system.

2. It has been shown on the basis of reported results from mating A $\times$ B, where no exceptions to Bernstein's theory can occur, that the product of frequencies of blood group A and blood group B, in nearly all reported cases, exceeds the product of frequencies of blood group

O and blood group AB, though these products should be numerically equal, or in other words the quotient $\frac{A \times B}{O \times AB}$ should be equal to unity. The result of analysis was rather disappointing with regard to the accuracy of serological technique applied by the majority of scientific workers who studied mating $A \times B$. The question was also asked whether the reported results from other matings could be considered reliable or whether they are similarly incorrect. It has been shown that exceptions to Bernstein's theory could be considered as errors, or that, on the contrary, their low frequencies could be equally explained by inaccuracy in testing. The latter possibility means that more reported exceptions might be expected in the future if more accurate technique is used.

3. The conclusion was reached that the existence of exceptions to Bernstein's theory could be rightly assumed. A modification of his theory was suggested while the basic frame of the theory was retained. In order to explain reported exceptions, it was suggested that genes A and B are partially linked. It is presumed that both genes A and B, being present simultaneously on the same chromosome, are mutually eliminated in their manifestation. In this connection it was mentioned that this supposed mutual action of genes, called position effect, could be compared to stereo-isomeres of the same molecules of proteins.

4. The formulae for estimating the relative frequencies of chromosomes were derived. The expected frequencies of children of respective blood groups resulting from each possible mating were given. These were expressed in terms of relative frequencies of chromosomes while linkage was also taken into account. The relative frequencies of blood groups in children resulting from all possible matings theoretically should be identical with relative frequencies of respective blood groups of the population of parents. The same should also be true regarding relative frequencies of chromosomes.

5. The relative frequencies of chromosomes actually calculated for an observed population of parents proved to be nearly equal to the relative frequencies calculated for the population of children. This coincidence was offered as a proof of the stability of population with regard to the blood groups in successive generations and also as a convincing proof of their Mendelian inheritance.

6. The linkage value was estimated by algebraic solution of equations where observed relative frequencies of cross-overs (e. g. exceptions to Bernstein's theory) were equated to their expected frequencies given in terms of known relative frequencies of chromosomes and unknown linkage value. Two systems of these equations were formed and solved for the unknown linkage value, one, by using all the exceptions of the same mating, the other, by using the exceptions only of the same blood group but resulting from all matings. The close coincidence of linkage values estimated separately for each mating, with the one exception of mating $O \times O$ has been pointed out. Linkage values estimated according to the exceptions reported in all other matings showed a surprisingly small variation. The average excluding the mating $O \times O$, was 0.055, which seems to be a more accurate linkage value than the average of values calculated from all matings (0.049). It has been suggested that the testing of children resulting from mating $O \times O$ was not without errors, as far as exceptions of blood group B and AB were concerned. It has also been pointed out that an erroneous interchange between blood group B and blood group AB may be rightly presumed.

7. The suggested modification has not been presented as an attempt to question the validity of Bernstein's theory but, on the contrary, this modification has been offered in order to show that both theories, the former theory of von Dungern and Hirszfeld, as well as the commonly accepted theory of Bernstein, can be connected in one system.

8. Finally, it has been suggested that the proposed modification may open a new approach with regard to the exceptions which have been considered only as errors but which might become more frequent with improved testing, at least as far as the exceptions in some matings are concerned. On the other hand, if the frequencies of the exceptions are actually very low, a small value of linkage is indicated.

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